Dynamics of nitrogen nutrition of coexisting dominant trees in mixed broad-leaved/Korean pine forest¹

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Abstract Chemical analysis of ammonium, nitrate and total nitrogen in tree leaves and roots and an in-vivo bioassay for nitrate reductase activity (NRA) were used to monitor the seasonal variations in nitrogen assimilation among four coexisting dominant tree species, including Pinus koraiensis, Tilia amurensis, Fraxinus mandshurica and Acer mono, in a virgin mixed broad-leaved/Korean pine (Pinus koraiensis) forest. The soil study included individual horizons of L+F (0-5 cm), Ah (5-11 cm) and Aw (11-25 cm). All four species had nitrate and ammonium in their roots and leaves, and also NRA in leaves. This indicated that these coexisting species were adapted to ammonium + nitrate nutrition. A negative correlation existed between nitrate use and ammonium use. Ammonium concentration was higher than that of nitrate in tree leaves and roots, and also in soils, which indicated climax woody species had a relative preference for ammonium nutrition. There was a positive relationship between tree nitrogen nutrition use and soil nitrogen nutrient supply. Utilization of ammonium and nitrate as well as the seasonal patterns differed significantly between the species. Peaks of ammonium, nitrate, NRA and total nitrogen in one species were therefore not necessarily synchronous with peaks in other species, and which indicated a species-specific seasonal use of nitrogen. The species-specific temporal differentiation in nitrogen use might reduce the competition between co-existing species and may be an important mechanism promoting stability of virgin mixed broad-leaved//Korean pine forest.

Key words: Mixed broad-leaved/Korean pine forest, Coexistence, Climax stability, Nitrogen nutrition.

Introduction

The capacity of woody plants to assimilate available nitrogen (nitrate and ammonium) has been well studied, especially in terms of habitat and species-related differences in nitrate and ammonium assimilation capacity (Addoms 1937; Hauck 1968; Al Gharbi et al. 1984; Lee et al. 1978; Tamm, 1991; Vitousek et al., 1982; Li et al. 1994a, 1994b, 1995) However, no study has focused on species-specific temporal variation in nitrate and ammonium assimilation among explicitly co-existing woody plants, even though temporal differentiation in the use of nitrate and ammonium may reduce nutrient competition and promote co-existence among woody plants.

In the mixed broad-leaved/Korean pine (*Pinus koraiensis*) forest, Li *et al.* (1994a; 1994b; 1995) found significant differences in nitrate and ammonium assimilation among coexisting dominance trees species including *Fraxinus. mandshurica*, *Pinus. koraiensis*, *Tillia. amurensis*, *Acer. mono*), which were all able to use nitrate and ammonium as N source. Our previous study was, however, done on a single occasion, and raised the question on which the

This study was performed in a virgin mixed broad-leaved/Korean pine forest. This forest type known as the typical mixed deciduous/conifer forest vegetation in Northeast of China is in climax, and this forest ecosystem is stable and can keep high productivity for a long time. It is also species-rich forests. The occurrence of a species-specific temporal component in use of nitrate and ammonium could be an important mechanism promoting the stability, high productivity and high species diversity typically found in this type of forest. Four coexisting species of dominant trees are included in this study and their tolerance degree is in increasing order of F. mandshurica → P. koraiensis → T. amurensis → A. mono (Yang et al. 1988). Chemical analysis of the ammonium, nitrate, and total nitrogen contents in tree leaves and roots and the in-vivo nitrate reductase activity (NRA) bioassay were used to monitor nitrate and ammonium utilization. Nitrate and ammonium supply in soil were also determined at the same time.

Methods

Four species of the dominant trees were individually sampled at monthly interval during the entire

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present study focuses, i.e. where there existed species-specific temporal patterns in nitrate and ammonium assimilation among co-existing woody plants.

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growing season in the virgin mixed broad-leaved/Korean pine forest, at 740 m above sea level in Changbai Mountain, in Northeastern China. For each species, more than five leaves and absorbing roots were sampled. The soil material was sampled at the same time from surface downward, according to natural horizon depths (L+F0-5 cm, Ah 5-11 cm, Aw11-25 cm, roots distribution was abundant in Ah horizon). All materials were sampled between 08:00 and 09:00 hours to reduce the possible effect on results. The phenology of the four tree species was also recorded, to search for a relationship between seasonal progression of growth and nitrogen assimilation.

Water content, nitrate and ammonium contents in the fresh material sampled were detected when they were fresh, and also NRA in leave and nitrate reductase activity in Ah horizon of soil. After drying, amount of total nitrogen was detected. More details of methods had been reported in our previous study (Li et al. 1995).

Results and discussion

Seasonal variations in nitrate and ammonium contents of soil

Contents of water, nitrate, ammonium and total nitrogen differed significantly between horizons of soil, decreased from surface downwards. There was a same variation trend among different horizon of soils, except total nitrogen content (Fig.1).

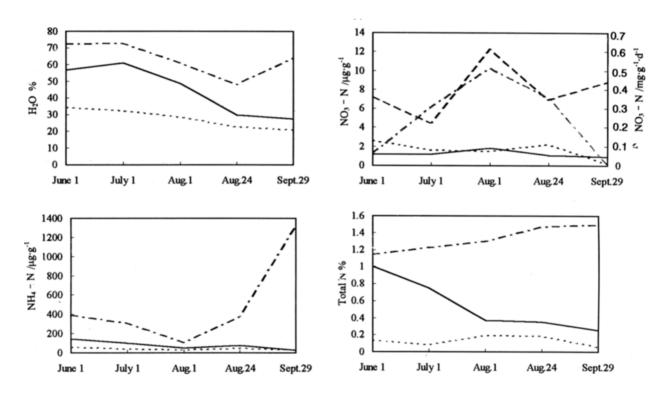


Fig. 1. The change of water content, NO₃ - N, NH₄ - N, total nitrogen content in the soil of broard-leaved/Korean pine forest

- - - - 0-5 cm; —— 5-11 cm; ····· 11-25 cm

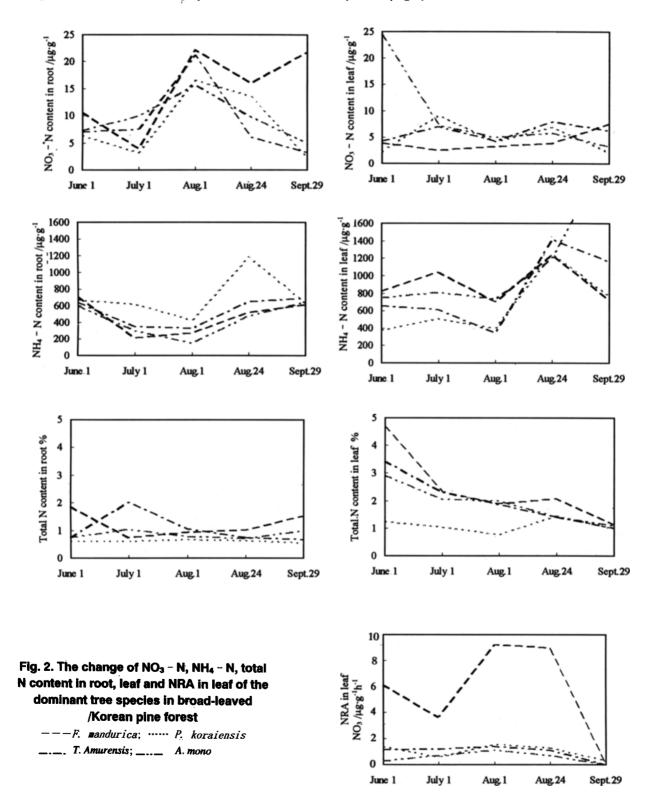
Highest contents of nitrate and ammonium in surface of soil (L+F 0-5 cm) could make greater contributions to the nitrate and ammonium supply of Ah horizon (5-11cm, roots distribution was abundant). Contents of nitrate and ammonium in Ah horizon of soil were influenced by some factors, increased by leaching from surface and mineralization of the soil and some other factors, decreased by absorption of plants and leaching into downwards in water. Nitrate and ammonium supply of soil were different and changed during the entire growing season. For example, content of ammonium was higher than that of

nitrate, decreased from the early of June to the early of Aug., but nitrate did not. Nitrate supply was good by the end of July and Aug, but ammonium was not. There was a positive relationship between nitrate content and nitrate redutase activity in Ah horizon of soil, because the variation trend was the same during the entire growing season. All above indicated that the ammonium was an important source of nitrogen in virgin mixed broad-leaved/Korean pine forest, the supply of nitrate and ammonium changed during the growing season. This would have influence on tree nitrogen nutrition.

Seasonal patterns in nitrate, ammonium and total nitrogen nutrient in coexisting dominant tree species

Nitrogen assimilation was highly variable, and the

utilization of nitrate and ammonium differed significantly between species. Although, all four species adapted to ammonium + nitrate nitrition, the ability in using nitrate and ammonium was different between species (Fig.2).



For example, F. mandshurica had higher ability in using nitrate than the others, because nitrate content

in root and NRA in leaves were higher, and also total nitrogen in leaves. P. koraiensis had higher ability

inusing ammonium than the other species, because ammonium content in root was higher, total nitrogen in roots and leaves and NRA in leaves was lower. Overall, F. mandshurica showed highest ability in using nitrate, followed by P. koraiensis, lowest T. amurensis and A. mono. There existed a negative relationship between ability of nitrate assimilation and tolerant degree. P. koraiensis showed highest ability in using ammonium, followed by T. amurensis and A. mono, lowest F. mandshurica. There was a negative relationship between nitrate and ammonium assimilation. As ammonium nutrition suppresses the absorption of nitrate, in all four species when the content of ammonium was highest in root, the nitrate was lowest. Although, peaks of nitrate in roots and NRA in leaves detected in early Aug. were the same to all four species, a peak of ammonium in roots in one species was not necessarily synchronous with peaks in the other species. For example, in F. mandshurica ammonium content had a peak by the end of Aug., while the others had peaks at beginning or the end of the growing season. This indicated a species-specific seasonal use of ammonium. Total nitrogen content in leaves was high at the beginning of the growing and generally decreased during the season, except P. koraiensis. There was a positive relationship between total nitrogen content and assimilation of nitrate, because nitrate absorption and reduction is an active energy dependent process and requires a great deal of energy.

Tree species' nitrogen assimilation is related to its phenology. The four species had different phenonlogical phase (Zou et al. 1998), but they all reguired more nitrogen nutrient in the time of flowering, fruit phase and also fast growth. For example, F. mandshurica requires more nitrogen nutrient when it was in the flowering period in June, in fruiting period in Sept. and fast growth of height in June i.e. nitrate, and ammonium content was relatively high in roots and leaves, also total nitrogen content in those periods. The other species were also the same. In view of our previous results, which showed nitrogen was the most growing limiting nutrient in the virgin mixed broad-leaved/Korean pine forest (Li et al. 1994a), it is likely that nitrogen availability limits tree growth in the forest. Consequently, as nitrate and ammonium are important sources of nitrogen, coexisting of dominant trees species in the virgin mixed broad-leaved /Korean pine forest should be favored by mechanism nitrogen nutrient competition. non-synchronous and species-specific use of available nitrogen (nitrate and ammonium) might be such a mechanism.

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